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lntrogression and Its Consequences in Plants

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Introgression and Its Consequences in Plants

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The role of introgression in plant evolution has been the subject of considerable discussion since the publication of Anderson's influential monograph, *Introgressive Hybridization* (Anderson, 1949). Anderson promoted the view, since widely held by botanists, that interspecific transfer of genes is a potent evolutionary force. He suggested that "the raw material for evolution brought about by introgression must greatly exceed the new genes produced directly by mutation" (1949, p. 102) and reasoned, as have many subsequent authors, that the resulting increases in genetic diversity and number of genetic combinations promote the development or acquisition of novel adaptations (Anderson, 1949, 1953; Stebbins, 1959; Rattenbury, 1962; Lewontin and Birch, 1966; Raven, 1976; Grant, 1981). In contrast to this "adaptationist" perspective, others have accorded little evolutionary significance to introgression, suggesting instead that it should be considered a primarily local phenomenon with only transient effects, a kind of "evolutionary noise" (Barber and Jackson, 1957; Randolph et al., 1967; Wagner, 1969, 1970; Hardin, 1975). One of the vociferous doubters of a significant role of hybridization in plant evolution was Wagner (1969, p. 785), who commented that the "ultimate contributions made by hybrids must be very small or negligible." Wagner's frequently expressed opinion appears to be based on ecological and compatibility arguments, which were encapsulated as follows: "In the rare cases that two well differentiated species happen to be interfertile enough to produce fertile progeny, their hybrids will usually have to fit into some hybrid niche. Such fertile hybrids will therefore tend to be transient, disappearing once the differentiated community returns and the parental species re-occupy their normal habitats" (Wagner, 1970, p. 149).

These divergent opinions primarily reflect differences in how various authors view the relative frequency of particular evolutionary outcomes, with few if any authors advocating the position that introgression *never* plays a significant evolutionary role. Anderson himself expressed uncertainty regarding its importance: "It is premature to attempt any generalizations as to the importance of introgressive hybridization in evolution" (1949, p. 61). Heiser was similarly equivocal, reaching the

conclusion that "Introgression does undoubtedly play a role in evolution. . . . It may play a very significant role; but it must be admitted, there is yet no strong evidence to support such a claim" (1973, p. 362).

In this chapter, we ask if any such "strong evidence" has accumulated since the last comprehensive review of plant introgression by Heiser nearly two decades ago and if any new perspectives or issues have been raised by empirical studies. We review evidence bearing on the extent of introgression in plants and its putative consequences. Particular emphasis is placed on insights gained from the application of molecular techniques, which provide the simply inherited genetic markers necessary to address many of the relevant questions but that were unavailable when the subject was last reviewed (see also Rieseberg and Brunsfeld, 1992). It is shown that these molecular data have greatly enhanced our ability to detect and quantify introgression, with perhaps a less dramatic influence on our ability to perceive its evolutionary consequences. We also review recent studies that have provided several insights into patterns and possible mechanisms of plant introgression.

WHAT IS INTROGRESSION?

The term "introgression" has been used to describe a wide range of phenomena, from backcrossing in hybrid swarms and breeding experiments to the exchange of genes between primarily allopatric species. Introgression or "introgressive hybridization" was first defined by Anderson and Hubricht (1938, p. 396) as "the infiltration of germ plasm from one species into another through repeated backcrossing of the hybrids to the parental species." Later authors (e.g., Stebbins, 1959; Heiser, 1973) suggested that the term be restricted to those situations involving the "permanent" addition of genes from one species into another, thereby attempting to draw a distinction between introgression and transient gene flow in local hybrid swarms. This distinction seems to us to be useful despite the difficulties inherent in assessing "permanence" of genetic transfer. Heiser (1973) pointed out that the term introgression need not apply only to results from backcrossing, inasmuch as the particular genetic history is likely to be unknown in most situations and because experimental data indicate that sib-crossing in conjunction with backcrossing is often superior to strict backcrossing for facilitating interspecific gene exchange (Wall, 1970). There is little rationale, in our opinion, for requiring any specific crossing scheme in a definition of introgression, regardless of issues of relative "efficiency." Although introgression was originally restricted to gene flow between species, it has been pointed out (Anderson, 1949; Heiser, 1973; Grant, 1981) that this definition is necessarily arbitrary owing to differences in species concepts among taxonomists. Furthermore, Anderson (1949) suggested that gene flow between intraspecific taxa represents essentially the same phenomenon as introgression between species. We concur and suggest that introgression can appropriately describe gene exchange between species, subspecies, races, or any other set of differentiated population systems. Given these considerations, introgression can be defined as the permanent incorporation of genes from one set of differentiated populations into another, i.e., the incorporation of alien alleles into a new, reproductively integrated population system.

When applying this definition to this review, we found it necessary to exclude from consideration certain evolutionary phenomena. The vast literature on local,

ephemeral hybrid swarms is not presented. With rare exception, hybridization leading to polyploidy is not discussed, despite the fact that it is one of the most prominent processes of plant speciation (Stebbins, 1950; Jackson, 1976; Lewis, 1980; Grant, 1981; Levin, 1983). Other than where it pertains to evolutionary issues, the vast literature on artificial hybridization and backcrossing in crop plants is omitted. Our discussion thus focuses on "natural" hybridization and introgression among diploid plants.

HISTORICAL PERSPECTIVE

Botanists have long been fascinated by plant hybridization, and the literature on this subject is voluminous. Excellent summaries of the early literature are given by Roberts (1929) and Heiser (1949a). Two of the earliest papers addressing the subject of introgression are those by DuRietz (1930) and Marsden-Jones (1930). DuRietz (1930) studied populations of *Dacrophyllum, Coprosma,* and *Salix* and noted that sympatric populations of certain species pairs tended to converge in certain morphological features. He attributed this convergence to the "infection" of one species with particular genes from another species. Marsden-Jones (1930) produced artificial hybrids between *Geum urbanum* and *G. rivale* and then backcrossed the hybrids to the parental species. He demonstrated that the backcrosses contained individuals that were almost indistinguishable from the parental species, confirming predictions made by Ostenfald (1928).

That introgression may have evolutionary implications, however, was first recognized by Edgar Anderson (Anderson, 1936a, 1949, 1953). In a series of papers on *Tradescantia* (Anderson and Diel, 1932; Anderson and Woodson, 1935; Anderson, 1936a, Anderson and Hubricht, 1938), Anderson and coworkers provided the first careful experimental studies of introgression, developed methods for its analysis (hybrid indices), introduced the term "introgressive hybridization," and suggested several possible consequences of introgression, including an increase in genetic diversity, the transfer of adaptations, and the development of new adaptations. They also were the first to explicitly recognize the relation between hybridization and the habitat (Anderson and Hubricht, 1938; Anderson, 1948). Anderson (1948) noted that different habitat preferences often form strong barriers to hybridization. Natural or human disturbance may remove these barriers, leading to extensive hybridization. In later papers (Anderson, 1949; Anderson and Gage, 1952), Anderson introduced additional methods for the detection of introgression, including the method of pictorialized scatter diagrams, which were widely used for several decades.

Anderson (1939, 1949, 1953) also introduced the concept of character coherence. Briefly, he suggested that linkage among genes affecting taxonomic characters results in strong correlations among these characters in the offspring of species hybrids. Thus hybrid indices and pictorialized scatter diagrams, in his view, provide an efficient means for analyzing suspected cases of introgression and for distinguishing the morphological results of introgression from those of convergent mutations or retention of ancestral character states. Although the concept of character coherence is still accepted by most plant taxonomists (e.g., Grant, 1981), theoretical and experimental studies (Dempster, 1949; Goodman, 1966) have indicated that factors other than linkage may also be responsible for taxonomic character correlations. For example, selective elim-

ination of recombinant types could result in strong character coherence regardless of linkage. In addition, if introgression is recent, correlations caused by overlapping hybrid and backcross generations can result in character correlations not generated by linkage alone (Goodman, 1966). Thus Goodman (1966) suggested that Andersonian techniques are applicable only in cases where it is known that there is no differential selection among recombinant and nonrecombinant chromosomal types.

This example typifies a problem that pervades the introgression literature; i.e., the supporting evidence often has alternative explanations (Gottlieb, 1972; Heiser, 1973). Many of these alternatives have been recognized for decades. Dobzhansky (1941), for example, recognized the implications presented by convergent morphological evolution. He also suggested the possibility that remnants of the ancestral population from which two species differentiated might have the appearance of hybrids—an early and explicit recognition of symplesiomorphy (retention of primitive character-states). It has also been recognized that primary intergradation could be difficult to distinguish from secondary intergradation. Barber and Jackson (1957), for example, questioned the traditional assumption that a steep cline—an abrupt change in a particular character or group of characters—always results from the merger of two previously differentiated populations. Baker (1947) was skeptical of the use of hybrid indices and other biometric tools in the absence of information regarding the genetic basis of the characters being scored. These and several additional explanations for variation patterns suggestive of introgression were discussed by Gottlieb (1972) and Heiser (1973), including segregation in a polyploid species, inbreeding and selection following hybridization in an autogamous species, the occurrence of hybrid swarms that are no longer in contact with the parental species, and the presence of highly variable F_1 hybrids. Given this panoply of potential problems, it is not surprising that Rieseberg et al. (1988a), following Heiser (1973), considered most putative examples of introgression to be based on circumstantial evidence.

Despite the inherent difficulties with adequately demonstrating introgression, there has been considerable discussion regarding its evolutionary significance. A recurring theme in many early studies of introgression was its importance as a source of genetic variation on which selection could act (Anderson, 1949, 1953). This view seems to have been accepted by many botanists. For example, Stebbins suggested that mutation can never provide enough variability to allow major evolutionary advances to take place: "Genetic recombination must, therefore, be the major source of such variability. . . . This is accomplished most effectively by mass hybridization between populations with different adaptive norms" (1959, p. 248). Rattenbury (1962) attributed the survival of tropical elements in the New Zealand flora to intermittent periods of hybridization (cyclic hybridization) and the production of variable offspring of which some could survive under cooler conditions. Knobloch (1972, p. 97) provided a list of 23,675 natural plant hybrids and states that "although mutation has been given the major role in effecting diversity in the natural world . . . , it is now quite clear to many biologists that the role of hybridization in speciation has been much larger." Likewise, Raven (1976, p. 298) suggested that "the formation of hybrids is a consistent feature of the adaptive system in many, if not most, groups of plants." As mentioned above, this point of view has not met with universal acceptance (Barber and Jackson, 1957; Randolph et al., 1967; Wagner, 1969, 1970; Hardin, 1975).

Many of the "modern" contributions to the study of introgression have been

methodological. The use of secondary chemical compounds (e.g., Alston and Turner, 1962; Flake et al., 1978) broadened the database available for the analysis of introgression. More recently, molecular evidence has been applied to the study of introgression, and it has been argued by several authors (e.g., Levin, 1975; Doebley, 1989a; Doebley and Wendel, 1989; Rieseberg and Brunsfeld, 1992) that molecular data are often preferable to morphological data for analyzing ambiguous cases of introgression because of (1) the ready availability of large numbers of independent molecular markers that allow the detection and quantification of even rare introgression; (2) the generally infrequent nonheritable molecular variation (Hillis, 1987); and (3) the apparent selective neutrality of many molecular markers (Kimura, 1982). In contrast, there are often few morphological characters differentiating hybridizing taxa, and these characters are often functionally or developmentally correlated. Moreover, morphological characters typically have an unknown, but presumably complicated, genetic basis, have a nonheritable component that is difficult to estimate, and often converge when exposed to similar selective pressures. Molecular markers also provide the opportunity to monitor both nuclear and cytoplasmic gene flow. Several authors have noted the advantages of employing chromosomally linked molecular markers for elucidating the direction of introgression and distinguishing it from symplesiomorphy and convergence (Avise and Saunders, 1984; Doebley, 1989a; Doebley and Wendel, 1989; Rieseberg et al., 1990a). The use of linked markers greatly increases the potential for the *simultaneous* appearance of multiple markers in an introgressed individual. Clearly, if a putative introgressant possessed multiple, linked markers of a potential hybridizer, the probability that this situation could be attributed to symplesiomorphy or convergence would be minimized.

Although molecular markers clearly provide an important alternative to morphological characters for the study of introgression, there are potential problems, particularly for multigene families such as the nuclear ribosomal RNA gene family (rDNA). Multigene families, which occur as tandem arrays or dispersed throughout the genome, are often subject to "concerted evolution," where sequences within a gene family are corrected against each other by processes such as unequal crossing over, gene conversion, slippage replication, or RNA-mediated exchanges (Drouin and Dover, 1990). If members of a multigene family are used to study introgression, these molecular processes may represent a serious source of error, as the frequency of the introgressed genes in an individual, population, or taxon could be increased or decreased because of this process. It is noteworthy that gene conversion has been experimentally demonstrated for rDNA (Hillis et al., 1991), a gene family often used in studies of introgression (e.g., Arnold et al., 1990a; Rieseberg et al., 1990a). Furthermore, biased gene conversion has been used to account for introgressive patterns of rDNA variation in grasshoppers (Arnold et al., 1988; Marchant et al., 1988), demonstrating the potential evolutionary significance of this phenomenon.

EXTENT OF INTROGRESSION IN PLANTS

To estimate the extent of introgression in nature, it is worthwhile to first examine the frequency of hybridization, as hybridization is a prerequisite to introgression. Naturally occurring interspecific hybrids have been detected in all major groups of plants and in all well-studied floras (Grant, 1981). Although only a small fraction of the plant

kingdom has been examined in detail and numerous hybrids go unreported, Knobloch (1972) was able to list 23,675 putative interspecific or intergenetic hybrids. It is more difficult to estimate the frequency of introgression in plants owing to the difficulty of obtaining unambiguous evidence (as discussed in this chapter). Nonetheless, we have attempted to list "noteworthy" cases of introgression in plants (Table 4-1) so as to: (1) provide a reasonably broad introduction to the primary literature; (2) illustrate the breadth of the phenomenon with respect to taxonomic groups and life history features; and (3) summarize the types of empirical evidence used in documenting introgression as well as its proposed consequences. This list is by no means exhaustive, and we have undoubtedly missed many noteworthy examples. In addition, we have included several studies where previously hypothesized examples of introgression have been examined and disproved (e.g., Rieseberg et al., 1988a; Spooner et al., 1991), because these "negative" papers play a role in clarifying the introgression literature.

Table 4-1 lists 165 proposed cases of introgression, many involving more than one species. The examples include one fern *(Trichomanes)* and the full spectrum of seed plant diversity, including three genera in two families of gymnosperms *(Abies, Pinus, Juniperus)* and 82 genera in 40 families of angiosperms. Within angiosperms, approximately 85% of the examples are from dicotyledonous families (34 families, 71 genera), including representatives from all dicot subclasses. Twelve genera in six families of monocots are also represented. Nearly all growth forms, which range from annuals to perennials and trees to herbs, are included. Many pollination syndromes are represented, with wind pollination being rarer than various forms of animal pollination. This finding perhaps runs counter to expectations based on the physical promiscuity inherent in the former, relative to the frequent specificity of the latter. Mating system variation also covers the full spectrum from obligate outcrossers to predominant selfers.

Each study listed in Table 4-1 was evaluated with respect to whether introgression had been rigorously documented in the sense that alternative explanations (see above) were eliminated. In general, we had greater confidence in those studies that employed molecular characters (see above for rationale) or employed numerous morphological, cytological, or chemical characters. Our judgment was that introgression had been documented in 65 cases. Other studies included in Table 4-1 substantiate the existence of hybrid swarms and *may* represent examples of introgression (denoted by "?"). We did not believe, however, that the "permanent addition" of alleles from another species was unambiguously demonstrated in these cases.

In his 1973 review, Heiser distinguished localized introgression, where gene flow extends only a short distance from the area of hybridization, from dispersed introgression, where gene flow is widespread (Fig. 4-1). He suggested that localized introgression is common, but dispersed introgression is rare. Although most of the examples on this list undoubtedly represent instances of localized introgression (denoted by "L"), several cases of dispersed introgression have now been documented as well ("D" in Table 4-1). This distinction, however, is not easily drawn. As pointed out previously (Rieseberg and Brunsfeld, 1991), it is difficult to determine whether apparent patterns of dispersed introgression represent widespread gene flow or result from the establishment and spread of stabilized introgressants (Fig. 4-1). That is, the genetic constitution of introgressed populations occurring away from the area of contact may be the same regardless of the process by which they were derived. Similarly, in cases where localized

Table 4-1. Proposed Examples of Introgression in Plants

Taxon	Evidence[a]	Introgression?[b]	Proposed Consequences[c]	References
Abies borisii-regis	M	?	S	Mattfeld (1930)
Acer saccharophorum/nigrum	M	?	T	Dansereau & Desmarais (1947)
Achillea roseo-alba	M,C	?	S	Ehrendorfer (1959)
Adenostoma fasciculatum	M	?	I,T	Anderson (1954)
Aegilops species	M	?	I,O	Feldman (1965)
Aesculus species	I,M,C	D	I	Hardin (1957); dePamphilis and Wyatt (1989, 1990)
Amaranthus species	M,C	?	B,E	Sauer (1957); Tucker and Sauer (1958)
Apocynum species	M,C	?	I	Anderson (1936b)
Aquilegia formosa/pubescens	M,E	?	I	Grant (1952); Chase and Raven (1975)
Arctostaphylos viscida/patula	I	L	n.a.	Ellstrand et al. (1987)
Argyranthemum sundingii	M	?	S	Brochmann (1987)
Argyranthemum coronopifolium/frutescens	M	L	B	Brochmann (1984)
Argyroxiphium grayanum	P	yes	n.a.	Baldwin et al. (1990)
Ascepias exaltata/syriaca	M	?	I,O	Kephart et al. (1988)
Asclepias speciosa/syriaca	S,I	?	n.a.	Adams et al. (1987)
Asclepias tuberosa	M	?	n.a.	Woodson (1947, 1962); Wyatt and Antonovics (1981)
Aster multiflorus/novae-angliae	M	?	I	Wetmore and Delisle (1939)
Bothriochloa intermedia	M	?	T,C	Harlan and de Wet (1963)
Brassica napus	P,[R]	yes	n.a.	Erickson et al. (1983); Palmer et al. (1983); Palmer (1988); Song et al. (1988)
Bromus pumpellianus/inermis	M	?	T,E,C	Elliott (1949)
Calyptridium monospermum	M	?	R	Hinton (1976)
Carduus nutans/acanthoides	M,I,P,R,S,C,	L	n.a.	Warwick et al. (1989)
Ceonothus species	M,C	?	E,T,S	McMinn (1944)
Cercis canadensis	M	?	T,I	Anderson (1953)
Cercocarpus traskiae	M,I	L	B	Rieseberg et al. (1989)
Cinchona species	M	?	T,O	Camp (1948)
Cistus species	M	?	S,E	Dansereau (1941)
Citrullus lanatus/colocynthis	I	L	n.a.	Zamir et al. (1984)
Clarkia bottae	M,C	?	S	Lewis and Lewis (1955)

Clarkia sect. *Fibula*	P,M	?	S,O	Lewis and Lewis (1955); Sytsma et al. (1990)
Clarkia speciosa ssp. *polyantha*	C,I,M	yes	E	Bloom (1976); Soltis (1985)
Cucurbita species	M,I	?	n.a.	Decker-Walters et al. (1990)
Cucurbita pepo/texana	I	L	n.a.	Decker and Wilson (1987); Kirkpatrick and Wilson (1988)
Cypripedium candidum/pubescens	M,I	L	E,T	Klier et al. (unpublished data)
Delphinium gypsophilum	M,C	?	S	Lewis and Epling (1959)
Diplacus species	C,M,E	?	I,E	Beeks (1962)
Dubautia scabra	P,S	L	n.a.	Crins et al. (1988); Baldwin et al. (1990)
Elymus species	M	?	I,E	Brown and Pratt (1960)
Elymus glaucus	M,C	?	S	Snyder (1950, 1951); Stebbins (1957)
Epimedium trifoliatobinatum	M,C	?	S	Suzuki (1986)
Eucalyptus risdonii/amygdalina	M	?	D	Potts and Reid (1988)
Fuchsia perscendens	P,[M]	?	n.a.	Sytsma et al. (1991)
Galium dumosum	M	?	S	Ehrendorfer (1958)
Gaillardia pulchella	I,S	L	n.a.	Heywood and Levin (1984); Heywood (1986)
Geum urbanum/rivale	C,M	?	n.a.	Ravanko (1979)
Gilia species	M,C	?	O,S,E	Grant (1953)
Gilia schilleaefolia	M,C	?	S	Grant (1954)
Gilia cana asp. *speciosa*	M,C	?	E	Grant and Grant (1960)
Gilia capitata ssp.	M,C	?	S,E	Grant (1950)
Gilia latiflora ssp. *davyi*	M,C	?	E	Grant and Grant (1960)
Gilia leptantha ssp. *transversa*	M,C	?	E	Grant and Grant (1960)
Gilia ochroleuca ssp. *vivida*	M,C	?	E	Grant and Grant (1960)
Gossypium bickii	P,[R,I]	yes	S,O	Wendel et al. (1991)
Gossypium aridum	P	yes	n.a.	Wendel and Albert (1991)
Gossypium arboreum	I	yes	I	Wendel et al. (1989)
Gossypium barbadense	I	yes	I,R,T	Percy and Wendel (1990)
Gossypium cunninghamii	P	yes	n.a.	Wendel and Albert (1992)
Gossypium darwinii	I	yes	n.a.	Wendel and Percy (1990)
Gossypium herbaceum	I	yes	I	Wendel et al. (1989)
Gossypium hirsutum	I	yes	R	Percy and Wendel (1990)
Helianthus annuus ssp. *texanus*	P,R,M,C	yes	T,E,C or N	Heiser (1951a); Rieseberg et al. (1990a)
Helianthus annuus	P,M,C	yes	T,E,C or N	Heiser (1947); Rieseberg et al., 1991a; Stebbins and Daly (1961)

Table 4-1. Proposed Examples of Introgression in Plants *Continued*

Taxon	Evidence[a]	Introgression?[b]	Proposed Consequences[c]	References
Helianthus anomalus	P,R,I	yes	O,S	Rieseberg (1991)
Helianthus argophyllus	M,C	?	T,E,C	Heiser (1951b)
Helianthus bolanderi	M,C,[P,R,I,S]	no	T,S	Heiser (1949b); Oliveri and Jain (1977); Rieseberg (1987); Rieseberg et al. (1988a,b)
Helianthus debilia ssp. *cucumerifolius*	P,R,M,C	yes	N	Heiser (1951a); Rieseberg et al. (1990a, 1991b)
Helianthus debilis ssp. *silvestris*	P,[R]	?	N	Rieseberg et al. (1991a)
Helianthus deserticola	P,R,I	yes	O,S	Rieseberg (1991)
Helianthus divaricatus/microcephalus	M	L	T	Heiser (1979)
Helianthus neglectus	P,[R,I]	yes	N	Rieseberg et al. (1990b)
Helianthus paradoxus	P,R,I	yes	O,S	Rieseberg et al. (1990b)
Helianthus petiolaris	P,R,M,C,	yes	T,E,C or N	Heiser (1947); Dorado et al. (1992)
Heuchera hallii	P	D	n.a.	Soltis et al. (1991)
Heuchera micrantha	P	yes	n.a.	Soltis et al. (1991)
Heuchera nivalis	P	D	n.a.	Soltis et al. (1991)
Heuchera parviflora	P	yes	n.a.	Soltis et al. (1991)
Impatiens aurella	M	?	T,S	Ornduff (1967)
Ipomopsis aggregate/tenuituba	M,S	L	n.a.	Grant and Wilken (1988)
Iris species	M,C	?	B	Lenz (1959)
Iris chrysophylla/tenax	S,[M]	L	n.a.	Carter and Brehm (1969)
Iris fulva/hexagona	R,M,C,E,I,N,[P]	D and L	O.T.	Riley (1938); Anderson (1949); Arnold et al. (1990a,b, 1991); Arnold et al. (1991)
Iris nelsonii	I,N	yes	S	Randolph (1965); Arnold et al. (1990b, 1991)
Juniperus ashei/virginianum	M,[S]	no	n.a.	Hall (1952); Flake et al. (1969); Adams and Turner (1970)
Juniperus virginianum/horizontalis	M	?	n.a.	Fassett (1945a,b)
Juniperus virginianum/scopularum	M,S	D	n.a.	Flake et al. (1978)
Juniperus scopularum/horizontalis	M	?	n.a.	Fassett (1945a,b)
Lasthenia burkei	M,C,[I]	?	S	Ornduff (1969, 1976); Crawford and Ornduff (1989)
Lasthenia ferrisiae	M,C	?	S	Ornduff (1966)
Lesquerella densipila/lescurii	C,M	L	n.a.	Rollins and Solbrig (1973)
Lesquerella densipila/stonensis	C,M	L	n.a.	Rollins and Solbrig (1973)

Lycopersicon esculentum var. esculentum	M,I	yes	n.a.	Rick (1958); Rick et al. (1974)
Lycopersicon chilense	P	?	n.a.	Palmer and Zamir (1982)
Lycopersicon chmielewskii	P	?	n.a.	Palmer and Zamir (1982)
Melandrium dioicum	M,C	?	E	Baker (1948)
Orphrys species	M	no	n.a.	Stebbins and Ferlan (1956)
Orphrys murbeckii	M	?	S	Stebbins and Ferlan (1956)
Oryza species	M,C,I	L	E,T,I	Chu and Oka (1970); Second (1982); Dally and Second (1990); Langevin et al. (1990)
Oxytropis albiflorus	M	?	T	Anderson (1953)
Parthenium argentatum	M	?	T,I	Rollins (1949)
Penstemon spectabilis	M	?	S,O	Straw (1955)
Penstemon clevelandii	M	?	S,O	Straw (1955)
Persea steyermarkii/P. nubigena	R,P	yes	S	Furnier et al. (1990)
Phlox anoena ssp. *lightipei*	M,C	?	E	Levin and Smith (1966)
Phlox bifida	M	?	I,T	Anderson and Gage (1952)
Phlox drummondii/cuspidata	I,M,C,[S]	L	N	Erbe and Turner (1962); Levin (1967, 1975)
Phlox divaricata ssp. *laphamii*	M,C	?	E	Levin (1967)
Phlox glaberrima/pilosa	I	L	n.a.	Levin and Schaal (1972)
Phlox maculata ssp. *pyramidalis*	M,Ph,S	?	E	Hadley and Levin (1969); Levin (1963, 1966)
Phlox pilosa ssp. *deameii*	M,C	?	E	Levin and Smith (1966)
Phytolacca species	M	?	S,E	Davis (1985)
Phytolacca species	M	?	T,C	Fassett and Sauer (1950)
Phytolacca americana	M	?	T,I	Anderson (1953)
Pinus contorta/banksiana	M,S,I,[P]	yes	n.a.	Forrest (1980); Critchfield (1985); Wagner et al. (1987); Wheeler and Guries (1987)
Pinus muricata	I	?	n.a.	Millar (1983)
Pisum sativum	P	?	n.a.	Palmer et al. (1985)
Populus fremontii/angustifolia	N	L	T	Keim et al. (1989)
Populus nigra	P,[R]	yes	n.a.	Smith and Sytsma (1990)
Potamogeton Xhaynesii	M,S	?	S	Haynes and Williams (1975); Hellquist and Crow (1986)
Potamogeton ogdenii	M,S	?	S	Hellquist and Hilton (1983)
Potentilla glandulosa ssp. *hansenii*	M,C	?	E	Clausen et al. (1940); Clausen and Hiesey (1958)
Primula vulgaris/elatior	M	?	n.a.	Valentine (1948)
Purshia tridentata/Cowania stansburyana	M	?	T	Stutz and Thomas (1964)
Purshia glandulosa	M	?	S,T	Stutz and Thomas (1964)

Table 4-1. Proposed Examples of Introgression in Plants *Continued*

Taxon	Evidence[a]	Introgression?[b]	Proposed Consequences[c]	References
Pyrrhopappus species	M,[I]	no	n.a.	Northington (1974); Peterson et al. (1990)
Quercus species	M	?	T,O	Muller (1952); Jensen and Eshbaugh (1976a,b)
Quercus alba	P,[M,R]	yes	n.a.	Hardin (1975); Whittemore and Schaal (1991)
Quercus alvordiana	M	?	S	Tucker (1952)
Quercus douglasii/turbinella	M	?	n.a.	Benson et al. (1967)
Quercus drummondii	M	?	S	Muller (1952)
Quercus dumosa/turbinella	M	?	n.a.	Tucker (1953)
Quercus durata	M,E	?	T	Forde and Farris (1962)
Quercus ganderi	M	?	S	Wolf (1944)
Quercus ilicifolia/marilandica	M	?	N	Stebbins et al. (1947)
Quercus macrocarpa	P,[R]	yes	n.a.	Whittemore and Schaal (1991)
Quercus marilandica/velutina	M	?	n.a.	Cooperrider (1957)
Quercus michauxii	P,[R]	yes	n.a.	Whittemore and Schaal (1991)
Quercus rober/petraea	M	?	n.a.	Rushton (1979)
Quercus stellata	P,[R]	yes	n.a.	Whittemore and Schaal (1991)
Ranunculus species	M,E	?	I	Briggs (1962)
Ranunculus victoriensis	M,E	?	S	Briggs (1962)
Raphanus sativus	M,C	?	T,I	Panetos and Baker (1967)
Sabatia formosa/arenicola	M,I,E	L	n.a.	Bell and Lester (1978)
Salix melanopsis	P,[I]	yes	n.a.	Brunsfeld (1990)
S. taxifolia	P,I,M	yes	S	Brunsfeld (1990)
Salvia mellifera/apiana	M	L	I,N,E	Epling (1947); Meyn and Emboden (1987)
Scaevola gaudichaudiana/mollis	M	?	I	Gillett (1966)
Solanum species	M,S	?	I,C,T,S,A	Hawkins (1962); Johns et al. (1987)
Solanum raphanifolium	M,[R,P]	no	S	Ugent (1970); Spooner et al. (1991)
Solidago rugosa/sempervirens	M	?	I	Goodwin (1937)
Stephanomeria diegensis	I	yes	S	Gallez and Gottlieb (1982)
Stipa californica	M	?	S	Johnson (1962)
Tellima grandiflora	P,[I]	yes	n.a.	Soltis et al. (1991)
Tradescantia occidentalis	M	?	T	Anderson and Hubricht (1938)

Trichomanes species	M	?	n.a.	Bierhorst (1977)
Triticum turgidum	C,P	?	T,S	Gill and Chen (1987)
Typha latifolia/angustifolia	M	?	I	Fassett and Calhoun (1952)
Vaccinium corymbosum	M	?	S	Camp (1945)
Viola species	M,C	?	T,O	Russell (1954); Moore (1959)
Viola cuculata/septentrionalis	M	?	n.a.	Russell (1955)
Wyethia species	M	?	T	Weber (1946)
Zea mays ssp. *mays/Z. mays* ssp. *mexicana*	M,P,I	yes	n.a.	Doebley et al. (1987); Doebley and Sisco (1989)
Zea mays ssp. *mays/Z. mays* var. *parviglumis*	M,[C,E,I]	no	n.a.	Kato (1976, 1984); Wilkes (1977); Doebley (1984); Doebley et al. (1984, 1987)
Zea perennis	P,[M,I,C]	yes	n.a.	Doebley (1989a)
Zea luxurians/Z. mays ssp. *mays*	I	yes	n.a.	Doebley et al. (1984)
Zea diploperennis/Z. mays ssp. *mays*	I,[C,E]	yes	n.a.	Doebley (1984); Doebley et al. (1984)

[a]C = cytological or crossing studies; E = ecological; I = isozymes; M = morphological; N = random, nuclear DNA markers; R = ribosomal DNA; P = chloroplast DNA; ph = physiological studies; S = secondary compounds. Letters in brackets refer to approaches employed for which no evidence of introgression was observed.

[b]Yes = introgression probably documented; L = local introgression; D = dispersed introgression. A question mark is indicated for cases where, in our judgment, interpretations other than introgression were not adequately ruled out.

[c]B = breakdown of reproductive barriers; D = dispersal mechanism; C = colonization; E = origin of new ecotypes; I = increase in genetic diversity; N = evolutionary noise; O = origin of adaptations; R = reinforcement of reproductive barriers; S = origin of new species or variety; T = transfer of adaptations; n.a. = no consequences proposed by authors.

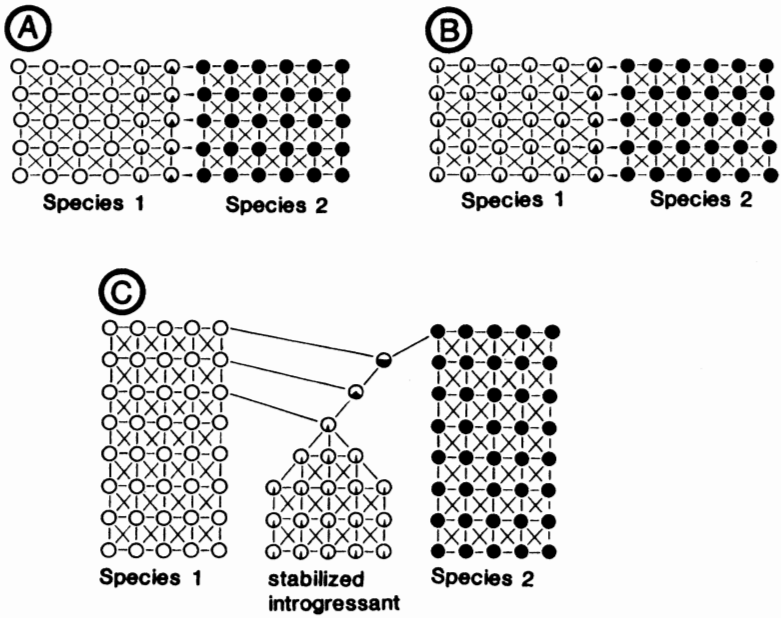

Figure 4-1. Localized introgression, dispersed introgression, and the origin of a stabilized introgressant. Open circles = populations of species 1; closed circles = populations of species 2; black lines = crosses between populations; arrows = direction of introgression. (**A**) Unidirectional localized introgression from species 2 into species 1. (**B**) Unidirectional dispersed introgression. (**C**) Origin of a stabilized introgressant.

introgression is apparent, dispersed introgression may have occurred but in a manner that could not be detected by the methods employed.

More than 90% of the examples listed in Table 4-1 are from temperate regions of the world. This bias undoubtedly reflects the location of scientists who have been interested in the phenomenon. Consequently, it is difficult to extrapolate to tropical plants. Likewise, approximately 25% of the cases listed in Table 4-1 are from California. This disproportionately high figure is due largely to the number of botanists in California, although the species and habitat richness of the California flora may also contribute to the observed high frequency.

A correlation between ecological stability and the occurrence and consequences of hybridization has long been apparent (Anderson and Hubricht, 1938; Dansereau, 1941; Anderson, 1948; Stebbins, 1959; Arnold et al., 1990a). The importance of ecological factors is twofold. First, ecological differences often result in barriers to hybridization (Anderson, 1948). If these barriers are broken down due to natural disturbance (e.g., fire, flood, volcanic activity) or human disturbance, hybridization often follows. Second, the establishment of hybrids and their progeny appears to be aided by relaxed competition in disturbed or open habitats. Thus introgressive hybridization is thought to be promoted by highly disturbed habitats such as those resulting from human activities (e.g., Anderson, 1948; Lenz, 1959). Many examples of introgression listed in Table 4-1 appear to be a direct result of natural or human habitat disturbance (Epling,

1947; Anderson, 1948; Sauer, 1957; Tucker and Sauer, 1958; Lenz, 1959; Stebbins and Daly, 1961; Heiser, 1979; Arnold et al., 1990a,b; Klier et al., 1991).

Although the focus of this chapter concerns introgression between wild species, introgression between wild and domesticated plants is suspected to be common (Anderson, 1949; Harlan, 1965; Heiser, 1973; deWet and Harlan, 1975; Ladizinsky, 1985; Doebley, 1989b) and provides some of the best cases of introgression in plants (Table 4-1). Molecular evidence for introgression has been reported in populations of *Brassica* (Erickson et al., 1983; Palmer et al., 1983; Palmer, 1988; Song et al., 1988), *Chenopodium* (Wilson, 1990b), *Citrullus* (Zamir et al., 1984), *Cucurbita* (Decker and Wilson, 1987; Wilson, 1990a), *Gossypium* (Wendel et al., 1989; Percy and Wendel, 1990; Wendel and Percy, 1990), *Helianthus* (Rieseberg and Seiler, 1990), *Lycopersicon* (Rick et al., 1974; Palmer and Zamir, 1982), *Oryza* (Chu and Oka, 1970; Second, 1982; Langevin et al., 1990), *Pisum* (Palmer et al., 1985), and *Zea* (Doebley et al., 1984, 1987; Doebley, 1989a; Doebley and Sisco, 1989).

It is often thought that introgression between crop plants and their weedy relatives is primarily unidirectional, with gene flow proceeding from the cultigen into the wild or weedy relative (deWet and Harlan, 1975; Ladizinsky, 1985; however, see Doebley, 1989b, for a criticism of this view). Presumably this situation reflects culling of weed × crop hybrids prior to the next planting season. It has also been suggested that introgression from wild plants into domesticated ones has played an important role in the origin and development of the latter (Anderson, 1961; Harlan, 1965; Heiser, 1973; Wilson, 1990b). A complete treatment of this subject is beyond the scope of this review, but some of the complications and types of evidence used may be illustrated by the origin of cytoplasmic male sterility (CMS) in the cultivated sunflower. Stable sunflower CMS (CMS 89) was first discovered in an interspecific cross between *H. petiolaris* and *H. annuus* (Leclercq, 1969). This discovery enabled production of the commercial hybrid sunflower, resulting in dramatic increases in yield over older varieties. Subsequent cpDNA analysis of cultivated and wild populations of *Helianthus* indicated that hybrid sunflower cultivars had the chloroplast genome of *H. annuus,* not that of *H. petiolaris* (Rieseberg and Seiler, 1990), a surprising finding given that CMS 89 is derived from *H. petiolaris* (Leclercq, 1969). Because cpDNA is inherited maternally in *Helianthus* (Rieseberg et al., 1991a), the most likely explanation for the absence of *H. petiolaris* cpDNA genotypes in the hybrid sunflowers was that the source population for CMS 89 was an introgressive population of *H. petiolaris* and *H. annuus.* This hypothesis was confirmed by analysis of seven individuals from the source population of *H. petiolaris* from which CMS 89 was derived; all plants had the morphology and nuclear ribosomal RNA genes of *H. petiolaris* but the cpDNA patterns characteristic of *H. annuus.*

DIFFERENTIAL INTROGRESSION

One of the more surprising results of this survey concerns the relative frequency of cytoplasmic (mitochondria and chloroplast) versus nuclear introgression in plants (Rieseberg and Soltis, 1991). A total of 37 instances of cytoplasmic introgression are reported [all documented using chloroplast DNA (cpDNA) evidence]; of these cases, 29 are considered to represent robust demonstrations (Table 4-1). This number is

remarkably high given the little time that cpDNA variation has been amenable to study and the small sample sizes employed in most studies (one to few individuals per taxon). At least half of these examples were completely unexpected based on previous morphological treatments. Furthermore, in 18 of these cases, detailed analyses using isozymes, morphology, or nuclear ribosomal RNA genes (rDNA) failed to detect simultaneous introgression of nuclear genes (e.g., Palmer et al., 1983; Doebley, 1989a; Brunsfeld, 1990; Rieseberg et al., 1990b, 1991b; Smith and Sytsma, 1990; Rieseberg, 1991; Soltis et al., 1991; Wendel et al., 1991; Whittemore and Schaal, 1991).

For many of these cases, the discrepancy between nuclear and cytoplasmic evidence appears to reflect biphyletic or reticulate phylogenetic events. This phenomenon can be illustrated by the unusual evolutionary history of an Australian cotton species, *Gossypium bickii* (Wendel et al., 1991). *Gossypium bickii* is one of three arid zone species included in section *Hibiscoidea* (with *G. australe* and *G. nelsonii*). In contrast to expectations based on the distinctive shared morphology of the group, *G. bickii* possesses a chloroplast genome similar to that of *G. sturtianum* of section *Sturtia* (Fig. 4-2). Yet phylogenetic analysis of allozyme and nuclear rDNA markers indicate that the nuclear genome of *G. bickii* shares a more recent common ancestor with *G. australe* and *G. nelsonii* than it does with *G. sturtianum* (Fig. 4-2). Fifty-eight accessions were examined with reference to nuclear markers, but not a single diagnostic *G. sturtianum* nuclear marker was detected in the nuclear genome of *G. bickii.* Wendel et al. (1991) suggested that these data reflect an ancient hybridization event, with *G. sturtianum* (or a similar species) serving as the maternal parent in a cross with a paternal ancestor in the lineage leading to *G. australe* and *G. nelsonii.* The maternal nuclear genomic contribution may have been eliminated subsequently from the hybrid or its descendants. Lineage sorting is sometimes viewed as an alternative explanation to introgression for nuclear or cytoplasmic discordance, but it is implausible in this situation because of the high sequence divergence values observed between the cpDNAs of *G. sturtianum* and the *G. australe/G. nelsonii* clade.

The differential between cytoplasmic and nuclear gene flow has been addressed in greatest detail by Rieseberg and coworkers in the genus *Helianthus.* Rieseberg et al. (1990a, 1991b) employed cpDNA and nuclear rDNA markers to assess levels of nuclear and cytoplasmic gene flow between *H. annuus* and *H. debilis* ssp. *cucumerifolius* in eastern Texas. Chloroplast DNA and rDNA markers of *H. debilis* ssp. *cucumerifolius* were detected in, respectively, 10 and 16 plants of 154. *H. annuus* plants assayed. Thus levels of nuclear and cytoplasmic gene flow from *H. debilis* ssp. *cucumerifolius* into *H. annuus* were roughly equivalent. In contrast, 193 of the 262 plants of *H. debilis* ssp. *cucumerifolius* surveyed had the cpDNA genotype of *H. annuus,* where only eight individuals had alien rDNA markers. Interspecific flow of chloroplast genotypes from *H. annuus* into *H. debilis* ssp. *cucumerifolius* was approximately 10 times greater than that for nuclear rDNA markers.

Rieseberg et al. (1991b) attributed the asymmetric cpDNA flow to the greater abundance of *Helianthus annuus* in east Texas. Assuming *H. annuus* and *H. debilis* ssp. *cucumerifolius* have roughly equivalent dispersal rates, the greater abundance of *H. annuus* would result in a proportionately greater introduction of *H. annuus* achenes into *H. debilis* ssp. *cucumerifolius* populations than vice versa. The integrity of the nuclear genome would be maintained by selection against foreign nuclear genes coupled with the effects of linkage (below).

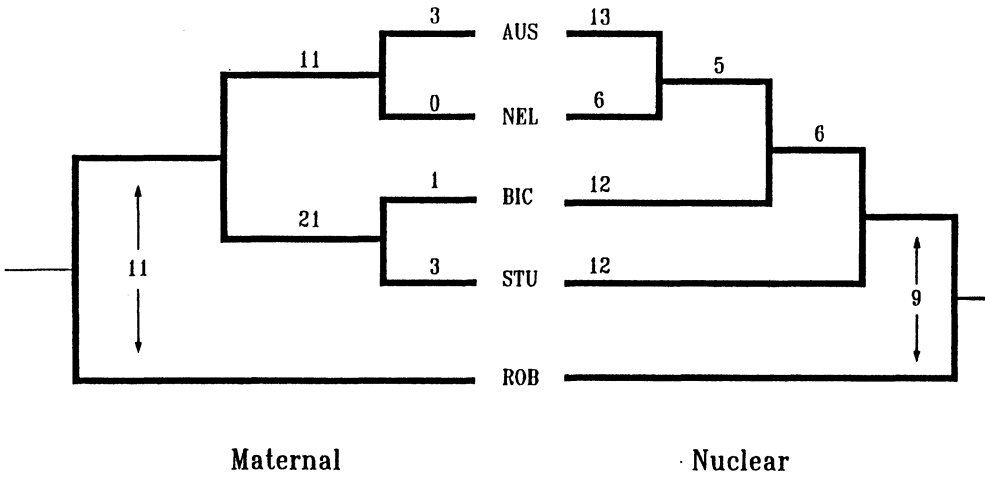

Figure 4-2. Discordant maternal and nuclear phylogenetic hypotheses of five species of Australian cotton *(Gossypium)* based on Wagner parsimony analysis. *Gossypium bickii, G. australe,* and *G. nelsonii* are monophyletic with respect to nuclear molecular markers (on right) and morphology (not shown). In contrast, evidence from chloroplast DNAs (on left) indicates a recent, shared common ancestry between *G. bickii* and G. sturtianum, the latter from a different taxonomic section. The maternal phylogeny was derived from restriction site loss/gain mutations in chloroplast DNAs (consistency index = 1.00). The nuclear tree was constructed from restriction site loss/gain mutations in 18S–25S ribosomal DNAs and presence/absence data for allozymes (CI = 0.81). In both trees, character states were polarized with respect to the outgroup species *G. robinsonii.* Arabic numerals indicate the number of nonhomoplasious synapomorphies or autapomorpies along each branch segment. AUS = *G. australe;* NEL = *G. nelsonii;* STU = *G. sturtianum;* BIC = *G. bickii;* ROB = *G. robinsonii.* (From Wendel et al., 1991. With permission.)

Analysis of cpDNA versus rDNA introgression between races of *H. annuus* and *H. petiolaris* from southern California also revealed that the interspecific flow of chloroplast genotypes was more frequent than that of nuclear ribosomal genes (Dorado et al., 1992). Both species are widespread and polytypic, occurring commonly in the western United States and less frequently eastward (Fig. 4-3). In California, *H. annuus* is a common roadside weed, occurring frequently in the central valley and in southern California. *Helianthus annuus* was already present in southern California when the first botanical collections were made and was used by native Americans for various purposes (Heiser, 1949b). Because it does not now occur in natural sites in either central or southern California, it was likely introduced recently by native Americans (Heiser, 1949b). *Helianthus petiolaris* represents an even more recent introduction to southern California, perhaps during the mid-1940s. According to herbarium records (RSA/POM), the first collections were made in 1947, and the species is now rather common. Yet all but four of the 141 individuals (six populations) of *H. petiolaris* analyzed from southern California had the chloroplast genotype of *H. annuus.* In contrast, only two plants had alien rDNA markers (Fig. 4-3). No introgression was observed from *H. petiolaris* into *H. annuus.* It is noteworthy that identification of "authentic" cpDNA genotypes of *H. annuus* and *H. petiolaris* was based on analysis of 51 popu-

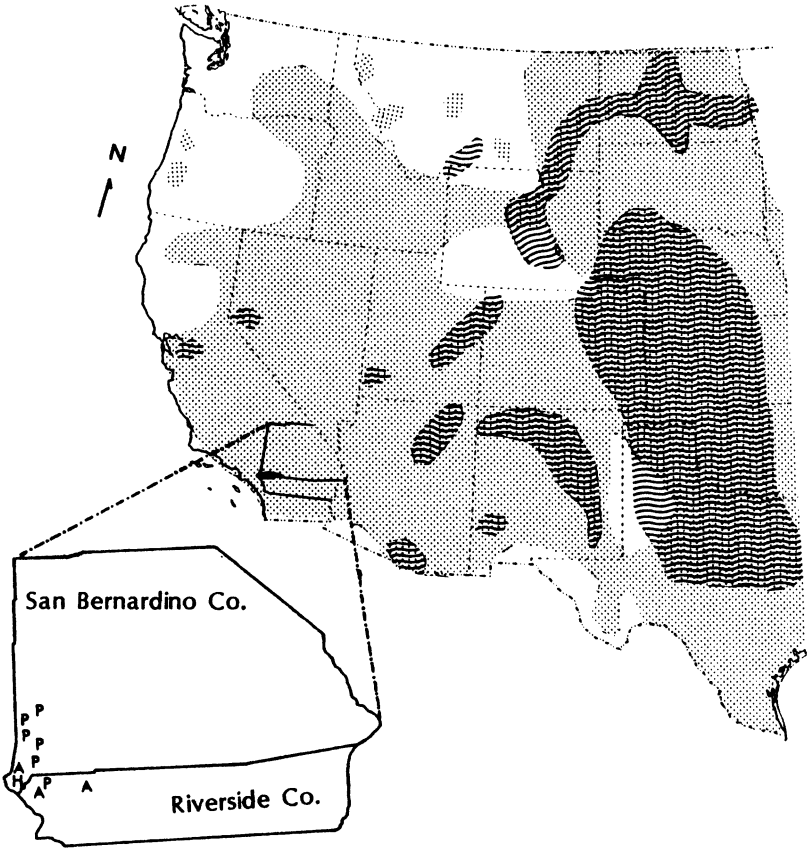

Figure 4-3. Geographic distribution and collection localities of *H. annuus* (dots) and *H. petiolaris* (wavy lines) in the western United States. A = *H. annuus* collection locality; P = *H. petiolaris* collection locality; H = hybrid population locality. (From Dorado et al., 1992. With permission.)

lations (212 individuals) and 12 populations (72 individuals), respectively, from throughout the range of both species (Rieseberg et al., 1991a). Thus misidentification of authentic *H. petiolaris* cpDNA cannot account for the observed situation.

Phylogenetic analysis of *Quercus* populations revealed a similar differential between organellar and nuclear gene flow (Whittemore and Schaal, 1991). A cladogram based on cpDNA data was congruent with geographic distribution rather than morphological species boundaries. Furthermore, the same cpDNA genotype was shared by individuals of two species growing in mixed stands. In contrast, rDNA marker distributions were consistent with morphology. Whittemore and Schaal (1991) suggested that nuclear genes may be exchanged less freely between species of oak than are chloroplast genomes.

Only two instances of nuclear introgression in the absence of cytoplasmic introgression have been reported in plants (Wagner et al., 1987; Arnold et al., 1991). Introgression of morphological features (Critchfield, 1985), terpenoids (Forrest, 1980),

and allozymes (Wheeler and Guries, 1987) has been detected between populations of *Pinus contorta* (lodgepole pine) and *Pinus banksiana* (jack pine). In contrast, extensive sampling of sympatric and allopatric populations (including some of the same populations used in the previous studies) with reference to species-specific cpDNA markers revealed no evidence of cytoplasmic introgression (Wagner et al., 1987). Likewise, examination of nuclear markers support a hypothesis of bidirectional nuclear introgression between *Iris fulva* and *I. hexagona* (Arnold et al., 1990a,b, 1991; see Ch. 5). Little cpDNA introgression was observed, however, suggesting that localized and dispersed introgression between these species is largely due to pollen transfer (Arnold et al., 1991).

Cytoplasmic and nuclear gene flow patterns are often different in animals as well, usually with cytoplasmic genes being exchanged more freely (e.g., Ferris et al., 1983; Powell, 1983; Carr et al., 1986; Gyllensten and Wilson, 1987; Tegelstrom, 1987; Marchant, 1988; Aubert and Solignac, 1990). In contrast, several studies have demonstrated roughly equivalent frequencies of nuclear and cytoplasmic gene flow (e.g., Avise et al., 1984; Syzmura et al., 1986; Harrison et al., 1987).

A number of hypotheses have been proposed to explain the different frequencies of cytoplasmic and nuclear gene flow in animals and plants (Barton and Jones, 1983; Powell, 1983; Gyllensten and Wilson, 1987; Aubert and Solignac, 1990; Rieseberg et al., 1991a,b; Wendel et al., 1991; Rieseberg and Soltis, 1991). One possibility is selection against alien nuclear genes but not against cytoplasmic genes (Barton and Jones, 1983; Powell, 1983). Selection against several loci scattered throughout the nuclear genome could greatly reduce overall nuclear gene flow due to linkage (Barton and Bengtsson, 1986; Whittemore and Schaal, 1991).

A second possibility is positive selection for cytoplasmic genes but not nuclear genes (Rieseberg et al., 1991a). Frank (1989) has shown that a native cytoplasm could be largely replaced by an alien one if the latter has a slight fitness advantage conferred by relative ovule success. This process would be promoted by cytoplasmic male sterility (CMS). In this aspect, it is noteworthy that CMS has been observed in a number of interspecific crosses in *Helianthus* (see Rieseberg and Seiler, 1990) and *Gossypium* (Meyer, 1975). Alternatively, differential gene flow could result from differential fitness among cytoplasmic-nuclear combinations (Wendel et al., 1991), whereby natural selection favors a particular alien/native cytoplasmic-nuclear combination.

A third possible mechanism, which may not be wholly separable from CMS, involves a small number of female immigrants of one species deposited into a population of another (Aubert and Solignac, 1990). Male sterility in first generation hybrids and first generation backcrosses could quickly lead to a small population of individuals containing alien cytoplasms. Individuals from subsequent generations would possess nuclear genomes that are increasingly indistinguishable from those of the host population. Similar results might be expected from the introduction of a hybrid, male-sterile propagule into a host population (Gyllensten and Wilson, 1987). This model may be the only one that can account for the *rapid* (< 50 years) replacement of the native *H. petiolaris* cytoplasm with that of *H. annuus* in the Southern California race of *H. petiolaris*. It is noteworthy that the first generation hybrids of *H. annuus* and *H. petiolaris* are sometimes male-sterile due to CMS (Rieseberg, unpublished).

Other mechanisms, such as semigamy, may promote unidirectional cytoplasmic introgression (Wendel et al., 1991). Semigamy is a form of facultative apomixis

whereby gamete fusion occurs without nuclear fusion, resulting in progeny that may include maternal haploids, paternal haploids, and chimeric maternal/paternal plants (Turcotte and Feaster, 1967). Wendel et al. (1991) pointed out that semigamy requires neither differential selection for cytotypes nor nuclear genes and can result in the fixation of the nuclear genome of a male donor into a foreign cytoplasm in a single generation. In this context, it may be significant that *Gossypium bickii* represents one of only two reasonably well-documented examples of the complete replacement of a native cytoplasm by an alien one (see also Smith and Sytsma, 1990).

Regardless of the mechanism responsible for cytoplasmic gene flow in the absence of significant nuclear gene flow, the process leads to several implications and conclusions. First, most botanists appear to accept the view that hybridization and introgression are frequent, yet ignore their potential implications for phylogenetic reconstruction [see Funk (1985) and McDade (1990) for notable exceptions]. Ironically, it is precisely this framework, i.e., the estimation of both nuclear and organellar phylogenies, that is responsible for the detection of many cases of introgression, although other evolutionary processes, such as random lineage sorting, can also result in patterns of discordance similar to those resulting from introgression. Nonetheless, the susceptibility of cytoplasmic organelles to introgression, which results in biphyletic organisms, suggests that caution be exercised in the use of organellar sequences for phylogenetic reconstruction. We suggest that an important area of future research is the development of algorithms for phylogeny reconstruction that are designed to account for reticulation.

Second, the degree of similarity between hybridizing species is potentially associated with their ability to exchange cytoplasms. Conversely, the effects of cytoplasmic exchange are more profound for divergent species than for closely related ones. One likely result is CMS, which is usually thought to arise from "incompatibility" between nuclear and cytoplasmic factors. It is also possible that cytoplasmic exchange between divergent species could lead to the formation of a new species as has been proposed for *G. bickii* (Wendel et al., 1991). Cytoplasmic transfer between closely related species generally has not been proposed as a common mechanism for speciation (e.g., Doebley, 1989a; Rieseberg et al., 1991a,b; Soltis et al., 1991; Whittemore and Schaal, 1991).

PROPOSED CONSEQUENCES OF INTROGRESSION

Evidence indicating that introgression is common in plants leads naturally to the question of its evolutionary significance. More specifically, which consequences of introgression, among the several envisioned by Anderson (1949) and others, are evident from empirical data? As indicated in Table 4-1, a number of consequences have been proposed, including increased genetic diversity, transfer of adaptations, origin of adaptations, origin of ecotypes or species, and breakdown or reinforcement of isolating barriers. Introgression has also been suggested as promoting colonization and as a dispersal mechanism (Potts and Reid, 1988). Each of these consequences is of potential interest from an evolutionary perspective. An additional consequence of an entirely different nature, however, emerges from phylogenetic considerations; i.e., introgression, by definition, involves reticulations, thereby rendering the reconstruction of evolutionary histories more difficult, regardless of specific biological conse-

quences. Finally, the possible escape of genetically engineered genes from crop plants through introgression into wild relatives provides an example of a potentially economically and environmentally significant consequence of introgression.

Evidence for each of the consequences listed above is discussed in the following paragraphs. These various consequences are not mutually exclusive; for example, the ability to colonize new habitats is expected to result from introgression of certain necessary adaptations.

Increase in Genetic Diversity. As discussed above, early authors saw introgression as an important source of genetic variation, noting that obviously introgressive populations should exhibit alleles of both parents as well as new single and multilocus genotypes. Thus estimates of genetic diversity calculated from molecular markers and morphological characters are expected to be higher in introgressant populations. Slightly less obvious is the prediction that new alleles may be produced through intragenic recombination or other processes (Golding and Strobeck, 1983). Irrespective of the potential generation of novel alleles, increased genetic diversity has been suggested as possibly altering adaptive potentials of introgressant populations (Lewontin and Birch, 1966).

We are aware of no evidence in the plant literature regarding the generation of novel alleles or "hybrizymes" (Woodruff, 1989) as a consequence of hybridization or introgression, in contrast to the animal literature where hybrizymes have been reported in hybrid zones involving mammals, birds, reptiles, amphibians, and insects (reviewed in Woodruff, 1989). Increased genetic diversity, though, is frequently reported in hybridizing plant populations. Hybridizing populations of white and yellow ladyslipper orchids (Cypripedium), for example, contain considerably higher morphological and allozyme variability than do allopatric populations of either species (Klier et al., 1991). Similarly, large increases in allelic polymorphism (up to 40% greater than the parental taxa) were observed in introgressive populations of three *Aesculus* species (dePamphilis and Wyatt, 1990). A modest increase in allozyme diversity was observed in introgressive populations of jack and lodgepole pines (Wheeler and Guries, 1987). In these and other studies, parallel increases in morphological and allozyme variability are often observed. This is not always the case, however. For example, introgressive populations of *Clarkia speciosa* spp. *polyantha* are no more variable morphologically than their parental taxa (Bloom, 1976), although there is a modest increase in allozyme diversity (Soltis, 1985).

With respect to genetic diversity predictions, it is important to distinguish between *recently* hybridized or introgressant populations (i.e., with recent biparental gene flow) and *stabilized* introgressants that are reproductively isolated from their parental taxa. In the latter, one might expect genetic drift or population bottlenecks to decrease genetic variability relative to progenitor populations, a prediction that has been confirmed for several species of hybrid or introgressant origin. In *Helianthus* (sunflowers), for example, dramatic decreases in overall genetic diversity were observed for three species of hybrid or introgressive origin: *H. anomalus, H. deserticola,* and *H. paradoxus* (Fig. 4-4) Rieseberg et al., 1990b, 1991; Rieseberg, 1991). *Helianthus paradoxus* and *H. deserticola* were polymorphic at only 1 of 17 loci examined, whereas *H. anomalus* was polymorphic at 3 of 17 loci. The number of polymorphic loci was much higher in parental species, ranging from four in *H. annuus* to seven

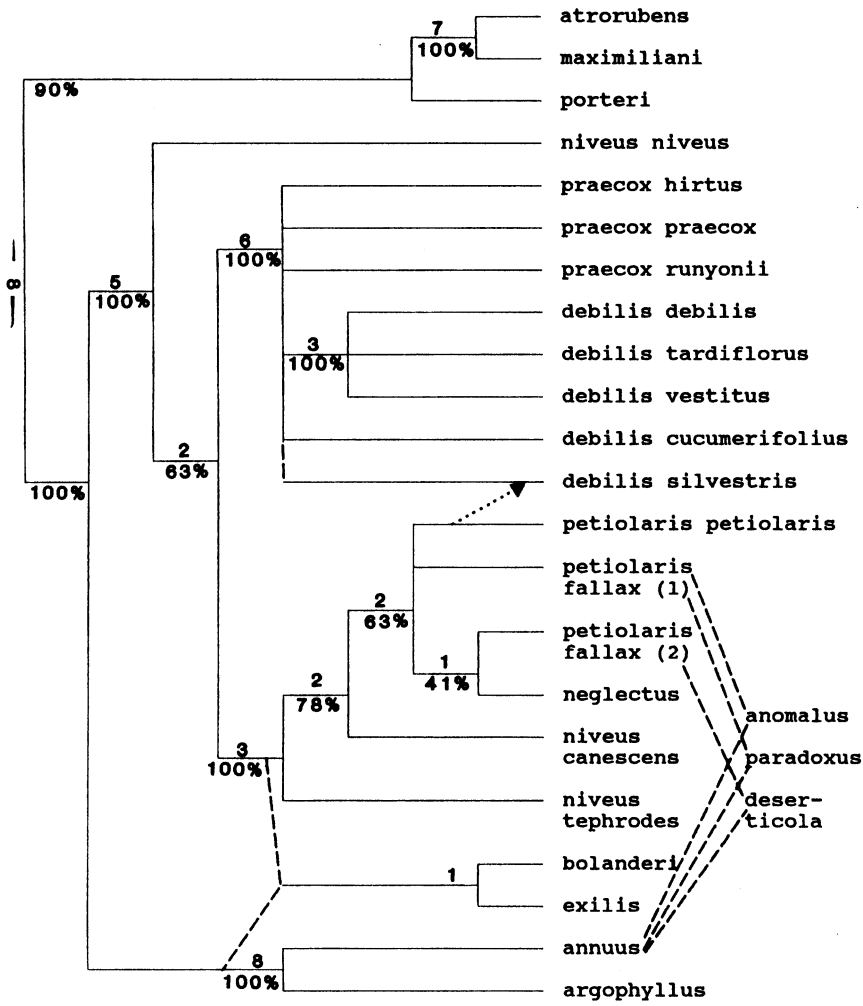

Figure 4-4. Phylogenetic estimate of *Helianthus* section *Helianthus* based on chloroplast DNA and nuclear ribosomal DNA variation. The phylogenetic tree was constructed as follows: (1) six taxa of biphyletic origin were removed from the data matrix: (2) Wagner parsimony analysis was performed on the remaining 19 taxa, resulting in the strict consensus tree presented in this figure; and (3) the six hybrid taxa were then added as parsimoniously as possible to the appropriate nodes of the consensus tree *(dashed lines)* demonstrating reticulate evolution. In the case of *H. debilis* ssp. *silvestris* the dashed lines simply indicate the capture of a foreign cytoplasm; no alien nuclear genes were detected. The consistency of the phylogenetic tree, including reticulations, was 0.85. Taxon designations are given at the ends of the branches, and the number of mutations are given above the branches. Autapomorphies are not shown. Percentages indicate the number of times a monophyletic group occurred in 100 bootstrap samples. (From Rieseberg, 1991. With permission.)

in *H. petiolaris.* Rieseberg et al. (1990b) attributed the low levels of genetic diversity to founder events following hybrid or "recombinational" speciation (Grant, 1981).

Increases in genetic diversity attributable to introgression have also been observed in several domesticated species of *Gossypium* (Wendel et al., 1989; Percy and Wendel, 1990). For example, at least 5 of 10 polymorphic loci in *G. herbaceum* (one of the two species of Old World cultivated cottons) are biallelic rather than monomorphic as a result of introgression (Wendel et al., 1989). A similar, though less extreme, effect is probable with the other Old World cultivated cotton, *G. arboreum;* perhaps 3 or 4 of 11 polymorphic loci are polymorphic owing to introgression (Wendel et al., 1989). Introgression also appears to have contributed to allelic diversity in improved varieties of one of the New World cultivated cottons, *G. barbadense.* Of the 20 polymorphic loci detected in cultivars of *G. barbadense,* nine were polymorphic owing to introgression alone (Percy and Wendel, 1990). Thus introgression appears to be responsible for much of the genetic diversity observed in cultivated cottons.

Transfer of Adaptations. A potentially significant consequence of introgression, transfer of adaptation, has often been proposed, but it is a difficult process to verify experimentally. Even when introgression has been "unambiguously" demonstrated, as with molecular data, it need not imply that adaptively significant genes were also transferred (Rieseberg et al., 1990a). It might be argued that the detection of introgression is synonymous with the transfer of adaptations, as hybrid zone theory predicts that advantageous alleles will cross species barriers more readily than neutral markers (Barton and Bengtsson, 1986). However, the great preponderance of "neutral" molecular markers relative to advantageous alleles leave us to consider this assumption premature. Furthermore, similar selection pressures could produce convergent morphological responses in certain adaptively significant features. It may be a common consequence of similar apomorphic tendencies in related species (Mayr, 1942). Finally, and most problematically, it is difficult to distinguish between transfer of adaptations and simple gene flow even where segregating admixtures contain individuals with morphological features of one species growing in the characteristic environment of the other. This general problem may be illustrated by ladyslipper orchid populations from Iowa (Klier et al., 1991). White and yellow ladyslipper orchid species are ecologically separated: The former occurs in prairies and other open vegetation types, and the latter is restricted to forest understory. Whenever the two species are parapatric in Iowa, they hybridize, resulting in the formation of hybrid swarms in the prairie. Allozyme and morphological data suggest that "yellow" ladyslipper individuals (i.e., morphological "yellows" containing no "white" marker alleles) occur in the prairie. The key question is whether the ability of these "yellows" to survive in the drier, brighter prairie has been transferred from white to yellow ladyslipper via differential selection on genetically recombinant progeny, or establishment of "yellows" in the prairie has been independent of these "white" genes. Distinguishing between these alternatives seems to require both an understanding of the genetic basis for habitat preference and reciprocal transplant studies on a variety of genetically defined parental and hybrid classes.

Despite these experimental difficulties, the literature contains several examples of putative interspecific transfer of adaptations (Table 4-1). Stutz and Thomas (1964), for example, suggested that the lowered palatability to herbivores of certain populations of *Purshia tridentata* has resulted from its acquisition of this characteristic via

introgression with *Cowania stansburyana.* The two species are sympatric in Utah, and hybridization is common wherever they come into contact. Although *Cowania* does not occur north of Utah, *Purshia* populations north of Utah express some of *Cowania*'s morphological characters. This situation is thought to have been promoted by some selective advantage for recombinant progeny, such as lowered palatability, which has been observed in a number of *Purshia* populations from the northern portion of its range. However, as pointed out by Heiser (1973), introgression is only one of several plausible explanations for this pattern of variation.

Helianthus provides several examples of the putative transfer of adaptations through introgression. For example, Heiser (1947, 1949b, 1951a,b, 1954, 1965) suggest that the most widespread species, *H. annuus,* was able to expand its range by introgression with native species already locally adapted. In his view, this process resulted in the formation of introgressive races varying toward *H. debilis, H. argophyllus, H. petiolaris,* and perhaps *H. bolanderi.* Molecular evidence provides some support for this interpretation, in that introgression between these species and *H. annuus,* as either the donor or recipient species, has been documented (Rieseberg et al., 1990a,b; Rieseberg, 1991). Likewise, Heiser (1951a) presented evidence suggesting that *H. annuus* was able to invade eastern Texas by "capturing" advantageous alleles of *H. debilis* ssp. *cucumerifolius,* a species already adapted to the area. Rieseberg et al. (1990a, p. 596) provided detailed molecular evidence for introgression in this case but noted that it "does not necessarily prove that the introgression of *H. debilis* ssp. *cucumerifolius* into *H. annuus* was in any way adaptive." In a more recent study, Heiser (1979) examined three hybrid populations of *H. divaricatus* (a species of open habitats) and *H. microcephalus* (a species found in shaded areas) over a 22-year period; considerable hybridity was still evident in one population at the end of this period, probably as a result of continued site disturbance. Although the habitat had become more closed at the other two sites, *H. divaricatus* was dominant at one site and the sole species found at the second site. Heiser suggested that *H. divaricatus* may owe its increased shade tolerance to introgression of genes from *H. microcephalus.*

Similar situations have been suggested for other plant groups. Harlan and deWet (1963) proposed that assimilation of local gene pools by *Bothriochloa intermedia,* a widespread grass species, allowed it to increase its geographic range and ecological tolerance. They introduced the term "compilospecies" to describe those species that, to use their imaginative expression, are "genetically aggressive, plundering related species of their heredities."

Origin of New Adaptations. It has long been evident that hybrids may have characters absent from both parents. Frequently cited examples include (1) bizarre corolla appendages in certain *Antirrhinum* crosses (Hagedoorn, 1921); (2) larger corollas in the hybrid of *Nicotiana langsdoorfi* × *alata* than those observed in either parent (Stebbins, 1966); and (3) novel secondary compounds in *Baptisia* (Alston and Simmons, 1962). Although it is difficult to assign an "adaptive value" to each character, it seems likely that these new characters will have novel adaptive potentials. These novel characters are thought to result from recombination among parental genes leading to novel multilocus genotypes, rather than the generation of new alleles. However, empirical evidence suggests that novel alleles or hybrizymes may also be produced by hybridization. For example, hybrizymes were observed in 19 of the 23 electrophoretic surveys

of hybrid zones reviewed by Barton and Hewitt (1985) and have now been reported for most major groups of animals (Woodruff, 1989). Several explanations of this observation have been proposed: increased mutation rates in hybrids, reduced selection, and intragenic recombination between different alleles of the parental species (reviewed in Golding and Strobeck, 1983, and Woodruff, 1989).

These new alleles and genetic combinations may be viewed as the "raw material for evolution" (Anderson, 1949). Experimental evidence that best supports this possibility comes from fruit flies rather than plants. Lewontin and Birch (1966) showed that introgressed populations of *Dacus tryoni* were better able to adapt to higher temperature regimens than populations of either parental species.

Although there are no comparable experimental studies in plants, there is circumstantial evidence for the origin of adaptations through hybridization. Rieseberg (1991) pointed out that the three stabilized hybrid derivatives of *Helianthus annuus* and *H. petiolaris* have notable ecological preferences. *Helianthus anomalus* and *H. deserticola* are xerically adapted sunflowers endemic to desert sand dunes and swales of the southwestern United States, whereas *H. paradoxus* occurs in brackish, saline, marshy areas in west Texas. Both of these habitats are extreme relative to either parent; *H. annuus* occurs in heavy soils that are saturated in the spring but dry by midsummer, and *H. petiolaris* occurs in drier, but not xeric, sandy soils. Riseberg (1991) suggested that these new ecological preferences "provide some support for the view of hybridization as a significant source of genetic novelty upon which selection can act."

Origin of New Types. The evolutionary consequences of hybridization and introgression most frequently emphasized by plant systematists is the generation of new homoploid taxa. In fact, nearly 40% of the examples listed in Table 4-1 propose the origin of a new ecotype or species as a consequence of introgression. These new types are often referred to as stabilized introgressants in the plant literature, i.e., populations that breed true for an alien allele (or alleles). Perhaps the first study to provide evidence that new ecotypes or species could be derived through introgression is that of Dansereau (1941) in the genus *Cistus.* Citing morphological evidence, he suggested that the North African variety of *C. ladaniferus* originated through the introgression of *C. laurifolias* into the typical variety of *C. ladaniferus,* which is restricted to the Iberian peninsula and southern France. *Cistus laurifolias* is sympatric with both varieties, first generation hybrids are often observed where the species occur together, and all the morphological differences that distinguish North African *C. ladaniferus* from typical *C. ladaniferus* are in the direction of *C. laurifolias.* The first detailed evidence for the origin of a new type through introgression was presented by Heiser (1949b) in *Helianthus.* He used morphological, cytological, genetic, and ecological data to postulate that a distinct weedy ecotype of *H. bolanderi,* a native sunflower of California, originated through introgression of genes from the recently introduced *H. annuus* into typical *H. bolanderi.* Ironically, molecular studies (Rieseberg et al., 1988a,b) have failed to confirm the occurrence of introgression in this case. In contrast, molecular evidence Rieseberg et al. (1990a) does support the hypothesized origin of *Helianthus annuus* ssp. *texanus* by the introduction of *H. annuus* into Texas and subsequent introgression of genes from *H. debilis* ssp. *cucumerifolius* into *H. annuus* (Heiser, 1951b).

The origin of stabilized new types through introgression has been suggested for many other groups of plants (Table 4-1). For example, Levin and coworkers postulate

an introgressive origin for *Phlox divaricata* ssp. *laphamii* (Levin, 1967), *P. maculata* ssp. *pyramidalis* (Levin, 1963, 1966), *P. pilosa* ssp. *deameii* (Levin and Smith, 1966), and *P. amoena* ssp. *lightipei* (Levin and Smith, 1966). Other genera with large numbers of proposed stabilized introgressants include *Gilia* (Grant, 1950, 1963; Grant and Grant, 1960), *Quercus* (Wolf, 1944; Muller, 1952; Tucker, 1952), and *Salix* (Brunsfeld, 1990). In addition, there are numerous examples where hybrid swarms or populations of stabilized introgressants appear to dominate disturbed or intermediate habitats: *Helianthus annuus/H. bolanderi* (Stebbins and Daly, 1961), *Helianthus divaricatus/H. microcephalus* (Heiser, 1979), *Iris fulva/I. hexagona* (Riley, 1938; Arnold et al., 1990a,b, 1991; see Ch. 5), *Salvia apiana/S. mellifera* (Epling, 1947; Meyn and Emboden, 1987), and *Cypripedium candidum/C. pubescens* (Klier et al., 1991). Many of these populations have been known to exist for more than 40 years, and there is no evidence to suggest that they are transient or ephemeral. Furthermore, in at least one instance (Stebbins and Daly, 1961), plants in the introgressive population appear to have formed a chromosomal sterility barrier isolating them from the parental taxa. It seems likely, therefore, that some of these populations represent the first stage of diploid hybrid speciation.

Models for the origin of new species through hybridization, without a change in chromosome number, have been developed by Grant (1949, 1958) and Stebbins (1957). Grant (1949) suggested that a new species could be derived through hybridization by the formation of an intermediate flower type and subsequent pollination by flower-constant insects. This mode of hybrid speciation, which has been postulated for two species of *Penstemon* (Straw, 1955), would most likely occur if backcrossing of the hybrids to the parents (introgression) is minimal. Alternatively, some other "external" isolating barrier could serve to isolate the hybrids from their parents (Grant, 1981).

A second model for the diploid hybrid origin of a species requires the development of chromosomal sterility barriers between the neospecies and its parents; this process has been termed "recombinational speciation" by Grant (1981). The basic model (Stebbins, 1957; Grant, 1958, 1981) can be summarized as follows: (1) Two parental species are distinguished by two or more separable chromosome rearrangements; (2) their partially sterile hybrid gives rise to new homozygous recombinant types for the rearrangements; and (3) the new recombinant types are fertile *inter se* but at least partially sterile with both parents. This model has been experimentally verified by the synthesis of new "hybrid" species in *Gilia* (Grant, 1966a,b), *Nicotiana* (Smith and Daly, 1959), *Elymus* (Stebbins, 1957), and *Crepis* (Gerrassimova, 1939). Furthermore, at least four wild plant species are now thought to have been derived through this process: *Stephanomeria diegensis* (Gallez and Gottlieb, 1982) and *Helianthus paradoxus, H. anomalus,* and *H. deserticola* (Fig. 4-4) (Rieseberg et al., 1990b; Rieseberg, 1991). In the latter three cases, the chromosomal sterility barriers isolating the hybrid species from their parents are known to be a consequence of their hybrid origin.

These two models clearly are not the only possible means by which reproductive isolation of a nascent hybrid taxon may occur. Other plant species, for which circumstantial evidence suggests a biphyletic origin (Table 4-1), may have been derived by the processes modeled above or by some other unknown mechanism. With respect to some species, however, it seems clear that neither of the above models is appropriate. For example, *Gossypium bickii,* which may have originated through an ancient hybrid speciation event (Wendel et al., 1991), is interfertile with its putative paternal lineage,

appears to lack chromosomal rearrangements, and has a floral morphology that is similar to one of its two putative parents.

Reproductive Barriers. Introgression is usually thought to reduce the strength of reproductive isolation barriers and sometimes even lead to the merger of two formerly isolated taxa (e.g., as in the compilospecies concept of Harlan and deWet, 1963). However, one potential outcome of hybridization is actual reinforcement of reproductive isolating mechanisms (see Ch. 3). It usually occurs through reproductive character displacement (e.g., Levin and Kerster, 1967; Levin, 1985; Whalen, 1978), which in the extreme should lead to a cessation of hybridization and therefore of introgression. Although reinforcement of isolating barriers is not generally associated with introgression, there are a few cases where introgression appears to be proceeding in one area of a species range and reproductive barrier reinforcement is taking place in another, e.g., *Calyptridium monospermum* (Hinton, 1976). Reproductive barrier reinforcement appears to have occurred in other plants, but these populations show traces of past introgression events, e.g., *B. barbadense/hirsutum* (Percy and Wendel, 1990).

There is relatively little evidence in the systematic literature for the breakdown of reproductive barriers through introgression, although natural or human disturbance has clearly ameliorated ecological barriers to hybridization and introgression in many genera (e.g., Anderson, 1948; Sauer, 1957; Tucker and Sauer, 1958; Lenz, 1959). Several long-term studies of introgressive populations are especially relevant (Stebbins and Daly, 1961; Hauber and Bloom, 1983; Meyn and Emboden, 1987). Stebbins and Daly (1961) examined an introgressive population of *H. bolanderi* and *H. annuus* over a 9-year period. The two species differ by three or four reciprocal translocations (Heiser, 1949b; Chandler et al., 1986), and first generation hybrids produce 2–10% stainable pollen. A 70–90% increase in pollen viability was observed in introgressive plants by the end of the 9-year period, suggesting a breakdown of chromosomal sterility barriers isolating these species. In a similar study, Meyn and Emboden (1987) compared pollen viabilities for hybrid populations of *Salvia apiana* and *S. mellifera* over a 30-year period and demonstrated that pollen viabilities of introgressed individuals now approach or even equal those of the parental species, whereas first generation hybrids generally have less than 50% stainable pollen. Perhaps the most striking example of the amelioration of chromosomal sterility barriers comes from a 10-year study of a chromosomal hybrid zone between *Clarkia nitens* and *Clarkia speciosa* ssp. *polyantha* (Bloom and Lewis, 1972; Bloom, 1976; Hauber and Bloom, 1983). They demonstrate that hybridization between these two chromosomally differentiated taxa has resulted in the production and establishment of new chromosome arrangements that serve to "genetically link" the parent species. These arrangements have become distributed geographically across the hybrid zone allowing for gene flow between the parental taxa with little loss of fertility.

Rieseberg et al. (1989) suggested that California's rarest tree, *Cercocarpus traskiae,* is in danger of extinction owing to genetic assimilation by its more widespread congener, *C. betuloides.* They pointed out that at least two and possibly as many as four of the seven remaining *C. traskiae* individuals are of hybrid or introgressive origin. Likewise, Brochmann (1984) provided evidence of possible extinction by swamping of *Argyranthemum coronopifolium,* a rare endemic that occurs in two disjunct areas in one of the Canary Islands. The common marguerite, *A. frutescens,* has

recently migrated as a weed along new roads into both areas of *A. coronopifolium* and forms extensive hybrid swarms with this species. We are not aware of other examples of plant species in danger of extinction due to introgression, although local extinction may be a frequent phenomenon. For example, *Cypripedium candidum* populations engaged in hybrid swarm formation with *C. pubescens* may no longer contain any "pure" individuals of the former species (Klier et al., 1991). A number of animal species appear to be endangered by introgression, including the cutthroat trout (Allendorf and Leary, 1988), Pecos pupfish (Echelle and Connor, 1989), yellow-crowned parakeet (Taylor, 1975), Seychelles turtle dove (Cade, 1983), Mexican duck (Heusmann, 1974), red wolf (Mech, 1970; Wane and Jenks, 1991), Mojave chub, and Tecopa pupfish (Soltz and Naiman, 1978).

Dispersal Mechanism. Potts and Reid (1988) suggested that hybridization via pollen dispersal may be of evolutionary significance as a means of gene dispersal where seed dispersal is more limited than pollen dispersal. They demonstrated that *Eucalyptus risdonii* is invading the range of *E. amygdalina* but suggested that the rate of colonization may be slowed by limited seed dispersal (Potts and Reid, 1985; Potts, 1986). Gene flow by pollen dispersal is suggested to be more widespread, however. Potts and Reid proposed that *E. risdonii* "appears to be invading favorable habitat islands by gene flow through the more widespread species, *E. amygdalina.*"

Schemske and Morgan (1990) criticized this conclusion based on the "very low frequency of hybridization, potential bias in estimation of distance of interspecific gene flow, lack of information on the extent of intraspecific pollen dispersal distances, and occurrence of comparable levels of hybridization in both species." They suggested that the hybridization observed between *E. amygdalina* and *E. risdonii* might be more realistically viewed as an accidental consequence of the evolutionary history of these two species, rather than as an evolutionary advantage arising from increased dispersal potential.

Phylogenetic and Taxonomic Consequences. Regardless of the adaptive importance of introgression, it is of great concern to practicing taxonomists and phylogeneticists (e.g., McDade, 1990). Introgression blurs taxonomic boundaries, leading to the common phenomenon of taxonomically "difficult groups." Hybridization and introgression have also influenced the development of various species concepts through the challenges they pose for the "biological species concept" (Cracraft, 1983; Donoghue, 1985; Ghiselin, 1987; Templeton, 1989).

Several authors have suggested that phylogenetic studies relying solely on variation patterns in organellar genomes (chloroplast and mitochondria) may be particularly susceptible to errors introduced by introgression (Doebley, 1989a; Furnier et al., 1990; Rieseberg et al., 1990a; Smith and Sytsma, 1990; Rieseberg and Soltis, 1991; Wendel et al., 1991). Three justifications for this conclusion may be offered. First, the maternal inheritance and vegetative segregation of organelles result in organellar genes having an effective population size that is approximately one-fourth that of nuclear genes (Birky et al., 1983), leading to a corresponding increase in the rate of fixation by drift and a decrease in expected gene diversity. Thus the likelihood of maintaining two divergent cpDNAs (native and alien) in a single population over long periods is less than for nuclear genes, with a corresponding decrease in the probability of detecting

and correctly diagnosing cytoplasmic introgression (Rieseberg and Soltis, 1991). Second, empirical evidence (discussed above; also see Table 4-1) indicates that nuclear genes may be exchanged less freely between species than organellar genes. Third, putative cases of biphylesis, involving strongly discordant organellar and nuclear phylogenies, are being reported with increasing frequency (Doebley, 1989a; Furnier et al., 1990; Smith and Sytsma, 1990; Rieseberg and Soltis, 1991; Rieseberg et al., 1991a,b; Wendel et al., 1991).

An example of the potential ease with which cytoplasmic introgression could lead to erroneous assessments of monophyly is provided by a detailed study of *Zea* (Doebley, 1989a). In this study, an atypical chloroplast genome was detected in eight individuals from one population ("Piedra Ancha") of *Z. perennis.* Comparison of the atypical cpDNA to other cpDNA types previously described for *Zea* (Doebley et al., 1987) revealed that this genome type was not present in any *Zea* species examined to date. Parsimony analysis indicated that the Piedra Ancha cpDNA genotype shares a most recent common ancestor with the plastid genomes of *Z. mays,* from which it is distinguished by five or six mutations. The cpDNAs from other populations of *Z. perennis,* however, are cladistically sister to *Z. diploperennis,* in accordance with traditional evidence and allozyme data. Doebley suggested that the foreign cytoplasm in the Piedra Ancha population was derived through introgression from some missing taxon. An erroneous phylogenetic conclusion could easily have been reached if Doebley (1989a) had failed to employ a comprehensive sampling strategy, or if he had failed to utilize evidence from nuclear genes.

Zea perennis is tetraploid, but the clade containing the Piedra Ancha plastome type consists solely of diploid species, except of course for the Piedra Ancha population of *Z. perennis.* Thus cytoplasmic introgression may have occurred across ploidy levels. Alternatively, the missing or extinct plastome donor was itself tetraploid.

Rieseberg and Soltis (1991) suggested a number of approaches to avoid erroneous phylogenetic conclusions based on cpDNA data. They included comparisons with phylogenetic hypotheses based on nuclear genes or morphological characters, comprehensive sampling strategies, and methods of data analysis that detect introgression events. At present, the latter consists primarily of conducting separate phylogenetic analysis of data from different genomes (e.g., Fig. 4-2), with subsequent examination of discordant clades. In the future, it may be possible to test for or hypothesize reticulation events using algorithms for phylogeny reconstruction that have been designed with this phenomenon in mind.

Introgression in Crop–Weed Complexes. One of the goals of plant breeding has been utilization of "exotic germplasm" via introgression of "useful" genes from wild relatives into breeding populations of the crop plant. This process traditionally has been restricted to the use of wild relatives with which the crop plant is interfertile, although somatic fusion of sexually incompatible plants is now possible. Advances in molecular biology have made possible the transfer of genes from organisms well outside the traditional crop gene pool through the use of recombinant DNA techniques rather than introgression via sexual processes (Gould, 1988). Thus plant breeders can introduce genes that contribute genetic resistance to specific diseases, herbicide tolerance, pests, and so forth. Although these techniques may undoubtedly lead to improvements in commercial crops, the potential for gene flow between crop plants and their wild or

weedy relatives has been demonstrated repeatedly (Table 4-1) providing a possible means of escape for genetically engineered genes. These data thus serve as a cautionary note to those involved in crop plant improvement via biotechnological means (Ellstrand, 1988; Wilson, 1990a). For example, introgression of genetically engineered herbicide resistance genes from crop plants to their weedy relatives could rapidly reduce the commercial value of an herbicide-resistant crop (Ellstrand, 1988).

PROBLEMS

We have reviewed the historical development of ideas regarding introgression in plants, examined the evidence for its extent, and discussed its potential consequences so as to assess its role in plant diversification and speciation. In this section, we discuss several problems that emerged from this review.

A general problem concerning the probability of detecting introgression is evident from the following considerations: (1) The likelihood of hybridization between taxa or differentiated populations, disregarding for the moment issues of opportunity, should, to a first order of approximation, be proportional to their degree of similarity; that is, closely related taxa should hybridize frequently, whereas phylogenetically more distant taxa do so only rarely. (2) The likelihood of detecting introgression should decrease as similarity between hybridizing taxa or populations increases as a consequence of the reduced availability of diagnostic molecular or morphological markers. (3) The likelihood of detecting introgression should decrease (by some unknown function) as the period of time elapsed since introgression increases. Reasons for this situation are threefold. First, the alien contribution is likely to be diluted over time. Second, mutations are likely to occur in the introgressed genes over time, making them difficult to identify. Third, the donor population or species may go extinct or change so dramatically in appearance and genetic constitution that its parental role may not be recognized and its genetic contribution difficult to detect or document.

These considerations have several implications. First, it is likely that a significant proportion of ongoing introgression is cryptic. With respect to evolutionary consequences, we would quote from the epilogue to Anderson's (1949) monograph, *Introgressive Hybridization:* "How important is introgressive hybridization? I do not know. One point seems fairly certain: its importance is paradoxical. The more imperceptible introgression becomes, the greater is its biological significance. . . . Hence our paradox. Introgression is of the greater biological significance, the less is the impact of casual inspection." Second, it is even more likely that a high proportion of historical introgression (i.e., between differentiated taxa that are not currently hybridizing) is cryptic. Third, only a small proportion of ancient introgression events are expected to be experimentally verifiable. In this respect, there is no reason to believe that introgression has not played a major role in the evolution of vascular plants in ancient as well as modern times. Indeed, Epling (1947) argued that the ability to hybridize may actually have been selected for in certain groups as an adaptation to rapidly changing environments (we do not hold this view). This point may have implications for phylogeny estimation at higher taxonomic levels. For example, Stebbins (1950) and Grant (1953) speculated that the lack of clear discontinuities between major evolutionary lineages of plants is a consequence of ancient hybridization events.

In conclusion, the evidence presented in Table 4-1, which indicates that introgression is extensive, may represent a gross underestimate of the true magnitude of the phenomenon in plants. By extension, we are most likely underestimating the significance of introgression in plant evolution. It is also likely that the available empirical evidence is biased toward recent introgression events and toward introgression between more distantly related taxa.

Particular difficulties arise when assessing the evolutionary consequence of ancient introgression events. For example, extensive introgression has been documented in several plant genera, including *Gossypium, Quercus, Helianthus,* and *Salix* (Table 4-1), yet we can only speculate regarding its consequences. Generally, if the origin of a new ecotype or species has been postulated as a consequence of introgression, as with the proposed hybrid origin of *G. bickii* (Wendell et al., 1991) and *Helianthus annuus* spp. *texanus* (Rieseberg et al., 1990), it is unclear whether introgression contributed to the *origin* of the new taxon or it occurred *afterward.* Failure to consider this scenario has frequently led to unjustified conclusions.

A final comment concerns a potentially significant question: Has introgression negatively or positively affected species richness in plants? Table 4-1 demonstrates that most botanists have suggested new ecotypes or species as a result of introgression rather than the breakdown of reproductive barriers or the merger of previously isolated taxa. Early botanists, however, tended to emphasize the potential "creative" role of introgression (e.g., Anderson, 1949; Stebbins, 1950), and it might be argued that their influence largely accounts for the bias observed in Table 4-1. Alternatively, the observed bias may result from the difficulty of demonstrating that a "merged" taxon actually originated from two taxa that are now extinct. In addition, from a mechanistic standpoint, hybridization and introgression may be viewed as a type of genetic recombination. Thus it might be argued that introgression, by expanding the field of recombination (Harrison, 1990), is an evolutionary force contributing to an increase in both genetic and taxonomic diversity. Testing this point of view must await the development of a clearer picture of both the extent of plant introgression and its evolutionary dynamics.

CONCLUSIONS AND FUTURE DIRECTIONS

In the last comprehensive review of plant introgression to date, Heiser (1973, p. 361) concluded that introgression exists but that "most introgression appears to be highly localized. In contrast, dispersed or widespread introgression ... appears to be extremely rare." Empirical evidence (Table 4-1) now available demonstrates that both localized and dispersed introgression occur, and we have indicated several reasons why frequencies of both types are likely to be underestimated. We also now have empirical evidence that introgression may contribute to an increase in genetic diversity, although the evidence for the transfer or origin of adaptations through introgression is less convincing. There are now many examples documenting that (1) populations of introgressants dominate disturbed or intermediate habitats, and (2) these populations are stable and may well contribute to the origin of new species. Furthermore, several diploid plant species are now known to be stabilized hybrid derivatives that were likely derived from ancient hybrid swarms or introgressive populations. Thus in our view

the evidence presented here indicates a major role for introgression in evolution, although it is recognized that much remains to be understood.

Molecular methodologies have contributed and will continue to contribute substantially to the detection and quantification of introgression (Rieseberg and Brunsfeld, 1992). Until recently, isozymes were the only molecular markers regularly employed in studies of introgression. A potential flaw of many studies has been the few nuclear markers surveyed, which in most cases range from one (rDNA) to several dozen (isozymes) genes. In the few cases where numerous molecular markers have been employed, little is known about the genomic distribution of successful introgressant alleles or their linkage relations.

These limitations are likely to be alleviated by technological developments that allow a virtually unlimited number of molecular markers to be scored. Restriction fragment analysis of low copy-number nuclear sequences (RFLPs) has been a readily accessible technique (for applications to the study of introgression see Keim et al., 1989; Song et al., 1988). Methodological gains hold the promise for even greater resolution. For example, PCR amplification of random oligonucleotide-primed DNAs (RAPDs) (Williams et al., 1990) may facilitate the detection and screening of numerous, highly variable molecular markers more efficiently than with current RFLP methods (Arnold et al., 1991). In addition to the many advantages afforded by the availability of a large number of markers, detailed genetic linkage maps may be constructed from single segregating progenies (e.g., Bernatsky and Tanksley, 1986; Helentjaris et al., 1986, 1988; Helentjaris, 1987; Tanksley et al., 1988; Michelmore et al., 1989). The advantage of using mapped molecular markers for the study of introgression is that the dynamics of not only individual markers but entire chromosomal segments can be monitored (Doebley and Wendel, 1989; Rieseberg and Brunsfeld, 1991). A significant capability is thus made available, i.e., ascertaining the genomic distribution of introgressed alleles and chromosome segments. For example, introgression may be restricted to a particular set of chromosomes or chromosome segments in a particular population. By establishing linkage relations between adaptively significant traits and molecular markers, the transfer of genetic adaptations can be documented with much greater precision, and hypotheses regarding the permeability of species barriers to advantageous, neutral, and disadvantageous alleles can be tested. This detailed genetic approach has the potential to enhance greatly our understanding of both the mechanisms and adaptive significance of introgression.

These methodological improvements are likely to have the greatest impact when combined with studies of the evolutionary ecology of hybrid and introgressive populations (see Ch. 5). Levin (1979) stressed the importance of experimental manipulations of hybrid swarms and hybrid zones, detailed comparisons of the biology of introgressive and parental plants in different environments, and estimates of fitness (e.g., pollen and seed dispersal) in hybridizing taxa. Similarly, Schemske and Morgan (1990) noted the importance of studying the full range of microevolutionary forces that may affect the direction and magnitude of gene flow. Rieseberg and Brunsfeld (1991) emphasized the need for examining the relative fitness of hybrids, introgressants, and parental plants in a range of environments, as well as studies that document the effects of introgression on isolating barriers. Sophisticated application of the tools of the evolutionary ecologist, when coupled with modern molecular methods, will undoubtedly significantly advance our understanding of introgression.

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